



Original Article

Competition decreases with relatedness and lek size in mole crickets: a role for kin selection?

Kit T. Keane,^a Warren Booth,^a Daniel R. Howard,^b Timothy M.J. Golden,^a and Peggy S.M. Hill^a

^aThe University of Tulsa, Department of Biological Science, Oliphant Hall Rm. 304, 800 S Tucker Drive, Tulsa, OK 74104, USA and ^bThe University of New Hampshire, Department of Biological Sciences, Spaulding Hall G32, 38 Academic Way, Durham, NH, 03824, USA

Received 17 July 2017; revised 30 April 2018; editorial decision 5 May 2018; accepted 15 May 2018.

Twenty years ago, Kokko and Lindstrom (1996) introduced the hypothesis that kin selection may drive the evolution of leks, shifting the lek-paradigm away from a competitive framework and spurring research on the relatedness of males on leks. However, support for Kokko and Lindstrom's kin-selection hypothesis has been sparse; most studies have shown related males to occur on leks no more than expected by chance. Additionally, evidence supporting the proposed mechanism is mixed; by joining a lek, males do not always increase the female visitation rate on a per-capita basis. The prairie mole cricket *Gryllotalpa major* is a lekking cricket in which male relatives advertise in close proximity. We reject the Kokko–Lindstrom hypothesis for this species because *G. major* females do not preferentially visit larger leks. Interestingly, more females visited smaller leks, where the presence of larger, more highly related males suggest reduced levels of local competition. Although the mechanism continues to be explored, these results provide an alternative inclusive fitness scenario to consider for lekking species—the existence of kin benefits between related neighbors rather than spread across the lek as a whole.

Key words: competition, female visitation, kin selection, lekking, prairie mole cricket, relatedness.

INTRODUCTION

Lekking is a mating system where males congregate in arenas or “leks” to advertise/display for females, yet offer them no resources besides sperm. Traditionally, lekking males have been thought to be in rigorous competition with one another for mating, though theoretical work has suggested the potential for kin selection to act among related males within a lek (Kokko and Lindstrom 1996). Males may achieve inclusive fitness benefits by lekking with close relatives, presumably increasing each other's attractiveness as they contribute to an increase in overall lek size, which is proposed to be more attractive to females (for a meta-analysis of female visitation rate and lek size, see Isvaran and Ponkshe 2013). A correlation between lek size and female visitation can result from many possibilities that are not associated with kin selection; however, such a correlation is required if Kokko and Lindstrom's kin-selection model is to be supported. Yet, for the benefits of increased female visitation to outweigh the cost of presumed increased competition in larger

leks, there must be a positive per-capita relationship between lek size and the number of female attractions, a pattern that is inconsistent across lekking species (Isvaran and Ponkshe 2013).

Several studies have addressed these concepts, yet there is no instance where a full dataset using the above logic has supported the existence of kin selection in a lekking system. Although studies of several systems have shown that related males lek together (Petrie et al. 1999; Shorey et al. 2000; Bouzat and Johnson 2004; Regnaut et al. 2006; Concannon et al. 2012; Keane et al. 2016), it is unknown whether female visitation or male copulation rate is correlated with lek size for these systems. Additionally, because relatives may be clustered when present on leks (Keane et al. 2016), we are interested in the possibility of a kin-selection scenario that does not involve spreading inclusive fitness benefits across the entire lek.

To evaluate the role of kin selection on leks, we use the lekking prairie mole cricket *Gryllotalpa major* Saussure as a model to test Kokko and Lindstrom's (1996) hypothesis by measuring whether female visits increase with lek size on a per-capita basis (Isvaran and Ponkshe 2013). A positive result does not confirm a role for kin selection in the evolution of the lek mating system, as a per-capita increase in female visits may result from a number of possibilities.

Address correspondence to K.T. Keane. E-mail: kristopher-keane@utulsa.edu.

Rather, if this trend of an increase in female visitation is absent, then we can refute Kokko and Lindstrom's hypothesis as a model for our test case. Because previous work has shown that *G. major* leks are comprised of multiple kin clusters (Keane et al. 2016), we explore the potential for kin-selected fitness benefits occurring within subgroups rather than across the lek as a whole. To assess this possibility, we examine leks of varying size and hypothesize that males in smaller leks will be 1) more closely related because they originate from only 1 or 2 broods and 2) experience reduced competition for food resources due to low population density.

G. major is a rare insect in which male relatives sexually advertise close to one another within larger aggregations for 30–40 min at sunset. Males call from individual subterranean burrows to females flying overhead (Walker and Figg 1990; Hill 1999; Keane et al. 2016). Individuals can detect conspecific male calls at least 80 m away (Hill 1998; Howard et al. 2011), a larger distance than males probably travel in their lifetime (Keane et al. 2016). Lifetime female visitation rates to individual males can be readily quantified, since males exhibit lek fidelity and even use the same burrow for up to weeks at a time during their single season of sexual advertisement (Figg et al. 1992; Hill 1999). Males only seem to use burrows they have constructed themselves, perhaps because they must be specifically tuned to the individual caller (Bennet-Clark 1987; Hill et al. 2006). In over 20 years of study, no physical aggression has been observed between males or females.

Male prairie mole crickets have been shown to be highly related to their immediate neighbors (Keane et al. 2016), which coincides with previous analyses of nearest-neighbor distances demonstrating spatial clustering of males (Hill 1999). Because male mole crickets are rarely observed in flight and females produce and care for a single brood per year (Lydekker 1896; Hayslip 1943; Loher and Dambach 1989), it is likely that males on small leks originate from only 1 or 2 broods. Thus, we expect small leks to show higher overall relatedness. Theory suggests that we may see increased competition for mates on smaller leks, but probably less competition for nutritional resources due to reduced population density.

We do not know where females of this species oviposit (except that they do not oviposit in the same burrow where they mate—see Hill 1999) or if they mate or fly on multiple nights. Previous work shows that female visitation to leks is highly concentrated over relatively few days (Howard et al. 2011). This suggests that males may frequently be able to take advantage of attendance gaps, caused when another male stops calling to engage in courtship, mating, or mate guarding, etc.—a duration known as “handling time” (Kokko et al. 2014). Although the longest *G. major* courtship song recorded was only about 9 min, males generally do not advertise again for the rest of the night's calling period, thus they probably do not mate with multiple females in a single night (Hill 2000). Similarly, due to the short calling period and the time constraints of mate searching, courtship, and spermatophore transfer, it is highly unlikely that females visit or mate with multiple males in a single evening. Unfortunately, because courtship occurs within the underground burrow, it is unknown if opportunities for sneaker and/or satellite strategies exist.

There are indications that behavioral interactions occur between neighbors. Males have been observed to adjust multiple aspects of their calling song in response to airborne and substrate-borne components of nearby calls (Hill and Shadley 2001). Males that display extremely close together (<1 m) tend to interrupt one another and thus are unable to call consistently, always resulting in at least one of the males excavating a new burrow further away (Hill 1996). After

landing, a female actively phonotaxes toward a male's burrow and changes direction to another nearby caller when her original choice stops calling (see [Supplementary Material](#)). Due to the high likelihood that neighbors are related, this occurrence more often than not benefits relatives of the original caller. It is unclear if mole crickets can actually identify their relatives, though kin recognition via chemical cues is known to occur in other crickets (Simmons 1989, 1990, 1991).

Although kin selection, based on inclusive fitness benefits shared among highly related neighbors, is a valid possibility, it has been questioned in cases, such as this, when population structure is the result of very low levels of dispersal (known as population viscosity; see Wilson et al. 1992; West et al. 2002). Kin-selected benefits in some mating scenarios may be effectively cancelled by the fitness cost caused by increased competition among relatives for mating opportunities and future competition between related offspring (Taylor 1992). Essentially, in a viscous environment, the negative effects of kin-competition are expected to trend proportionally with the benefits of neighbor relatedness. Therefore, we gauge whether the cost of potential kin-competition reduces the potential kin benefits in leks of different sizes—which we expect to display varying levels of relatedness. If increased kin-competition results from philopatry, we would predict that costs of competition evenly counterbalance inclusive fitness benefits, unless these benefits enable a larger population to exist on a given patch (elasticity—see Taylor 1992). Although we cannot differentiate kin-competition from that between nonkin, we are able to compare levels of competition with the average relatedness on a lek.

To indirectly evaluate the presence of competition, we gather data on male body condition, operational sex ratio, and an approximation of mating skew. Sex ratios and skew serve as proxies for adult mate competition; whereas, male body condition likely depends on competition for food resources and energy expenditure during both juvenile and adult life stages. Even though gut content analyses of several *G. major* males suggest a mainly plant based diet (Figg and Calvert 1987), individuals housed in lab settings prefer a more proteinaceous diet (unpublished data). Thus, it is possible that protein (e.g. invertebrate prey) is a limiting resource even though plant material comprises a majority of their diet. Dietary protein has been found to be an important macronutrient involved with weight gain in crickets (Harrison et al. 2014). In addition, we compare male and female relatedness-by-distance patterns in order to verify that females disperse freely in this species. High rates of female dispersal may significantly reduce overall population viscosity despite the inferred pattern of male philopatry in this species (Keane et al. 2016). It is possible, though perhaps unlikely, that male size is highly heritable rather than dependent on the environment, in which case it would not serve as an accurate representation of competition for nutritional resources. Unfortunately, a lack of parent-offspring data precludes any formal tests of heritability. Instead, we test whether more highly related males are likely to be similar in size.

Because small groups of *G. major* males within leks have already been shown to be significantly spatially aggregated at several scales (5 m, 7 m, and 11 m—see Hill 1999) and often consist of close relatives (Keane et al. 2016), the potential for kin selection between related neighbors is an intriguing possibility in this system. Competition for nutritional resources or mates probably does not occur across an entire lek, since elevated male relatedness suggests that males do not travel very far and are almost always found within 10–20 m of their siblings (Keane et al. 2016). Here, we test the patterns of relatedness, competition, and female visitation across leks

of varying size. Competing possibilities include 1) there is no link between competition, relatedness, and lek size, 2) competition and relatedness are positively correlated (this suggests that increased competition is a byproduct of male viscosity and that inclusive fitness benefits enable patches where relatives are present to support an increased number of individuals), or 3) relatedness and competition are negatively correlated (corresponding with a scenario for potential kin selection between immediate neighbors).

METHODS

Sampling

From 2013 to 2015, we visited 8 populations across *G. major*'s range comprised of 15 leks defined by a >100-m buffer, coinciding with the effective hearing range of male advertisement calls (Hill 1998; Howard et al. 2008). We collapsed 2 large aggregations of 53 and 32 burrows into 1 lek, because the distance between them was <120 m, close to our threshold (see lek ST, Table 1; Figure 1). A minimum count of actively displaying males was conducted for each site. We also provide a general estimate of the total number of calling males for larger leks due to the difficulty of differentiating calls of several males from a distance and ensuring that multiple surveyors do not double-count any individuals (a trained surveyor can usually count at least 20 males in an evening by locating each calling burrow). Smaller populations and those visited multiple times over a season tend to show more concordance between the minimum count and overall estimate. Because population numbers may not be precise, we divided observed leks into 3 general size classes, small (<15 males), medium (16–25 males), and large (>30 males). See Table 1 for all details pertaining to lek size.

We excavated calling burrows of 203 individual *G. major* males and removed a small tissue sample from the tips of the hind-wings for each male (including data for 98 males reported in Keane et al. 2016). Additionally, the precise location of male burrows was logged using a differential GPS unit (Trimble Navigation, Sunnyvale, CA) for most sampled males (except PB in 2013 and those for which flags were disturbed by wildlife) and all burrows with traps affixed (giving us precise coordinates for all females as

well). Mass at capture was recorded for most males ($N = 140$). There has been a precedent for using body mass as a size index in field crickets despite the fact that mass can fluctuate with the availability of water (Simmons 1986; Gray 1997; Ryder and Siva-Jothy 2001; Rantala and Roff 2005). We also documented several measures of male size, including head width, pronotal width, pronotal length, forewing length, and 2-dimensional abdominal-thoracic area ($n = 129$ for size traits). All size measurements were performed using ImageJ software (Schneider et al. 2012) and were collapsed into principal components along with mass using R (R Core Team 2016). See Supplementary Table S2 for PCA results.

Unlike some aboveground insects where mass can be highly variable depending on water availability, mole crickets have been observed to adjust their calling chamber depth in response to soil moisture (personal observation). Thus, mass for this group is likely less dependent on water availability and more correlated with energy reserves and availability of food resources. Male mass in this species has previously been found to correlate with call characteristics that are presumably under female evaluation, such as maximum amplitude and dominant frequency (Howard and Hill 2006).

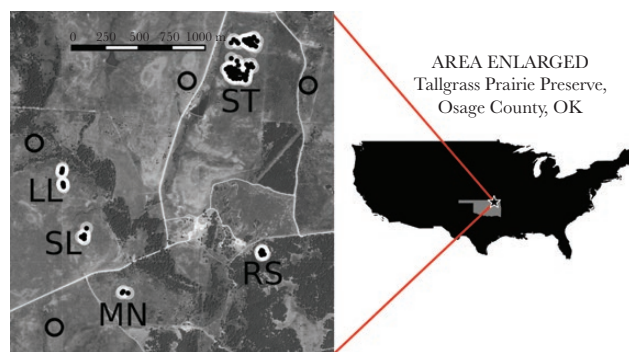


Figure 1

Aerial map of tallgrass prairie preserve. Map shows male burrows and corresponding lek abbreviation (see Table 1). Large, black circles indicate unstudied leks of unknown size during 2015. Created with QGIS using 2010 NAIP aerial images (QGIS Development Team 2012).

Table 1
Lek size and location

Lek	Abbreviation	Population	Number of males		Size class	Males sampled
			Minimum count	Overall estimate		
*Cherokee	CK	Cherokee Prairie, AR	29	50–75	L	11
*Downs	DN	Downs Prairie, AR	30	30–35	L	11
*Eufaula	EF	Eufaula State Park, OK	8	8–10	S	3
*Gray	GY	Gray Prairie, AR	20	20–25	M	6
*Friendly	FR	Paintbrush Prairie, MO	7	7–10	S	3
*Grandfather	GF	Paintbrush Prairie, MO	1	1	S	1
*Paintbrush	PB	Paintbrush Prairie, MO	30	35–40	L	22
Long Loop	LL	Tallgrass Prairie, OK	12	12	S	2
Mesonet	MN	Tallgrass Prairie, OK	3	4	S	3
Research Station	RS	Tallgrass Prairie, OK	8	8	S	5
Short Loop	SL	Tallgrass Prairie, OK	6	6	S	3
Spring Trap	ST	Tallgrass Prairie, OK	85	90	L	28
*Wa-Sha-She	WS	Wa-Sha-She Prairie, MO	14	15–20	M	3
White Oak North	WON	White Oak Prairie, OK	45	60	L	37
White Oak South	WOS	White Oak Prairie, OK	115	120	L	63

Lek names, abbreviations, locations and number of males counted. Starred sites were only visited 1–2 nights, whereas others were studied extensively over the duration of the calling period (20+ nights).

We calculated a body mass index (BMI) by regressing mass on the first principal component of the combined size measures (PC1 accounted for ~70% of the overall variance—see [Supplementary Material](#)). Regressing wet mass on linear measures of size has also been used as an index of condition even though there may be some issues that limit its usefulness ([García-Berthou 2001](#); [Green 2001](#); [Freckleton 2002](#); [Knapp and Knappová 2013](#)). Although residuals from a mass/length regression in insects are often substituted as a measure of adult energy expenditure, this ignores the linkage between size at eclosion and juvenile dietary environment, as has been observed for many orthopterans ([Hunt et al. 2004](#); [Hahn 2005](#); [Zajitschek et al. 2009](#); [Kelly and Tawes 2013](#)). Because no one measure of size is without its flaws, we chose to calculate all of the above measures and include them in our analysis.

To gauge female visitation rates, screened pitfall traps were placed over male burrows on 4 leks (LL, RS, SL, ST) at the Tallgrass Prairie Preserve during 2015 (TGPP; lat/long: 36.846212, -96.422731). Because we were able to measure only one large lek during 2015, we combine these data ($N = 88$) to previously gathered female attraction data from 2009 ($N = 38$, [Howard et al. 2011](#)) and 2010 ($N = 17$, Daniel R. Howard, unpublished data). See [Table 2](#) for leks sampled and numbers of females per lek. Although leks were trapped for unequal periods due to uneven patterns of male advertisement and disturbance of traps by grazing bison, all leks except RS were completely covered for the first ~2 weeks of the calling season, a period that coincides with a majority of female flight activity ([Howard et al. 2011](#), see [Table 2](#) under “#Calling Days”; female numbers for RS are thus likely an underestimate). We used *R* to test for differences in sex ratio between leks, initially employing a χ^2 -test to determine if significant deviations in sex ratio were present ([Newcombe 1998](#)), then the Marascuilo procedure for pairwise chi-square comparisons to identify which leks deviated from one another ([Marascuilo 1966](#); [R Core Team 2016](#)). Because we are unable to document the underground mating encounters for this species, we instead substitute “attraction” skew, which represents the number of females caught attempting to visit each male. We then tested whether attraction skew varies across leks. Values displayed in [Table 2](#) are *B* indices with 95% confidence intervals generated using Skew Calculator 2003 ([Nonacs 2000, 2003a, 2003b](#)).

Genotyping and population relatedness

To calculate relatedness, we used genotype data from 300 individuals collected at 14 different leks. This includes genetic information from 98 individuals reported previously ([Keane et al. 2016](#)). See [Supplementary Table S1](#) for the number of genotypes obtained from each population per year. Specimens were genotyped at 12 microsatellite loci following previously established methods for this species (and including genetic data reported in [Keane et al. 2016](#)).

One locus (GM-29) was flagged for potential linkage via Genepop ([Raymond and Rousset 1995](#)) and for null alleles by MICRO-CHECKER ([Van Oosterhout et al. 2004](#)), likely as a result of extreme variability, so we removed it from any further analysis. A heterozygote deficit was detected in all large leks where extensive sampling took place, indicative of substantial kin subdivision as previously shown for at least 1 population ([Keane et al. 2016](#)). We chose to remove only GM-29, because though significant overall patterns of linkage disequilibrium and null alleles were observed, in most instances they were driven by only 1 or 2 large populations, likely resulting from population subdivision (see [Supplementary Material](#) for genetic analysis data). All pairwise relatedness values presented were calculated using the Triadic method implemented in the program COANCESTRY ([Wang 2007, 2011](#)).

Histograms and Q-Q plots showed both mass/size and relatedness data to be nonnormally distributed ([Wilk and Gnanadesikan 1968](#)). Triadic relatedness data were nonnormal due to a bottom value of “0.” Thus, we used the Kruskal–Wallis (K–W) test to explore lek-size related differences in mass/size and relatedness ([McKight and Najab 2010](#)), followed up by Dunn’s test for post hoc pairwise comparisons ([Dunn 1964](#)). We also used a one-way Anova to check for a linear relationship between sex ratio and relatedness ($N = 4$ leks for which both sex ratio and relatedness data were available). Pearson’s product–moment correlation was calculated for relatedness-by-distance patterns ([Pearson 1895](#)). K–W tests for a linear correlation between relatedness and size similarity were performed in *R*.

RESULTS

Female attraction

Males called for 17 consecutive days in 2009, 22 out of 31 days in 2010, and 21 out of 34 days monitored in 2015. Males do not call in cold, windy, or rainy weather ([Hill 1998](#)). Similar to previous years ([Howard et al. 2011](#)), *G. major* female occurrence in 2015 was highly concentrated, with 84% (74/88) of the females visiting leks on only 4 nights. Sex ratios of leks displayed significant global variation (χ^2 -test, $P = 7.57e-09$). Smaller leks consistently achieved a significantly higher rate of per-capita female visits (except for lek RS, see [Tables 2](#) and 3). In contrast to males on small leks, most males on the large lek (ST) never attracted a female. Attraction skew was consistently higher on small leks ([Table 2](#)).

Male body size

Mass of sampled males ranged from 1.85 to 3.45 g. Measures of linear and polygonal size generally showed less variation, with the possible exception of thorax–abdomen area. Mean male body mass and size were found to be significantly lower in larger leks across

Table 2
Sex ratio and attraction skew

Lek-Year	Males	Females	#Calling Days	F:M Ratio	Attraction Skew (B)
LL-2009	65	38	17	0.58	0.021
LL-2010	40	17	22	0.43	-0.003
LL-2015	12	30	19	2.50	0.022
RS-2015	8	11	14	1.38	0.097
SL-2015	6	18	19	3.00	0.114
ST-2015	88	29	12	0.33	0.001

Attraction skew, female:male ratio (per-capita females), and number of males/females at indicated leks.

G. major's range; however, small and medium leks showed no significant difference from one another, likely due to small sample size for the latter (for mass see Figure 2a; K–W overall $P = 0.002$; Dunn's pairwise S|M $P = 0.269$, S|L $P = 0.002$, M|L $P = 0.011$; for size $P = 0.01$, S|M $P = 0.189$, S|L $P = 0.019$, M|L $P = 0.014$). Male BMI did not show a significant correlation with lek size (K–W overall $P = 0.06$). Pairwise relatedness was not shown to be correlated with any similarity in size for males (K–W overall $P = 0.2847$).

Population relatedness

Mean male pairwise relatedness displayed significant variation across lek sizes (K–W test $P < 0.001$, Figure 2b). Post hoc analysis shows that all size classes were significantly different from one another (Dunn's pairwise: S|M $P = 0.022$, S|L $P = 0.00$, M|L $P = 0.024$). Males at TGPP showed a significant negative relationship between relatedness and distance between individuals (Pearson Test $P = 1.03e-07$), as has been previously observed for a different population (Keane et al. 2016). In contrast, females did not display a significant relatedness by distance pattern (Pearson Test $P = 0.472$),

and the slope of the linear regression significantly diverged from that of males (Anova table model comparison $P = 3.88e-07$, see Figure 3). Tests for a linear correlation between relatedness and sex ratio were nonsignificant (Anova adjusted $R^2 = 0.609$, $P = 0.300$).

DISCUSSION

Our results fail to support Kokko and Lindstrom's kin-selection model for *G. major*, specifically its requirement for a per-capita increase in rate of female attraction to larger leks. This pattern is inconsistent across the species examined (Isvaran and Pongshe 2013), and we find a clear negative correlation between per-capita number of females and lek size in *G. major*. Some empirical support has been found for increased mean pairwise relatedness or the presence of close relatives within leks of other species (Lebigre et al. 2014), but where it has been found to exist, the lifetime patterns of female attraction are generally undocumented. Our data show that kin selection through female preference for lek size is unlikely to be a driving factor in the evolution of *G. major* leks. Interestingly, our

Table 3
Pairwise sex ratio differences

Pair	Size	Absolute difference (A)	Critical range (B)	A–B	Significance
RS15 ST15	S/L	0.331	0.4	–0.069	N
LL09 ST15	L/L	0.121	0.207	–0.085	N
RS15 LL10	S/S	0.281	0.427	–0.147	N
LL09 LL10	L/L	0.071	0.256	–0.186	N
LL10 ST15	L/L	0.05	0.241	–0.191	N
RS15 LL09	S/L	0.21	0.409	–0.199	N
LL15 RS15	S/S	0.135	0.443	–0.307	N
RS15 SL15	S/S	0.171	0.478	–0.307	N
LL15 SL15	S/S	0.036	0.375	–0.339	N
SL15 LL09	S/L	0.381	0.334	0.047	Y
LL15 LL09	S/L	0.345	0.281	0.065	Y
SL15 LL10	S/L	0.452	0.357	0.095	Y
LL15 LL10	S/L	0.416	0.307	0.109	Y
SL15 ST15	S/L	0.502	0.323	0.179	Y
LL15 ST15	S/L	0.466	0.267	0.199	Y

Significance of pairwise sex ratio (M:F) differences. Lek abbreviation and year are indicated (e.g. RS15 represents lek RS in 2015). Pairs in boldface represent tests between leks of different sizes. RS was the only lek that did not show significant size-based differences in sex ratios. Y: yes; N: no.

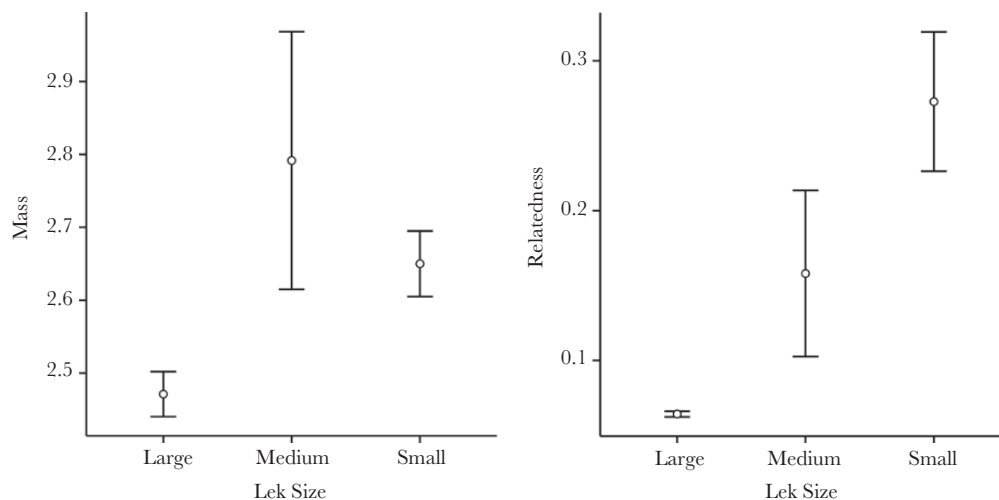


Figure 2

Male mass and relatedness by lek size. Point error plots showing the significant negative relationship between lek size and (a) male mass and (b) male–male relatedness. Bars represent standard error.

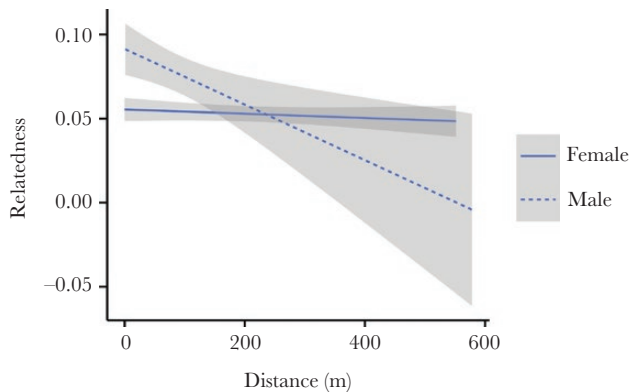


Figure 3

Relatedness by distance. Scatter plot with linear trend lines show a significant difference between the male and female relatedness-by-distance relationship. Shaded area represents standard error.

findings support the potential for inclusive fitness benefits at a different scale within leks.

Our data suggest lower levels of competition (higher male mass) on smaller leks where males are more related to one another. This is true for both nutritional resources and for mating opportunities. Lek size and relatedness negatively correlate both with mean male mass/size and the per-capita number of females. Unfortunately, a low sample size precluded us from teasing apart the relationship between these variables and sex ratio ($N = 4$ leks for which all 4 variables are available). This suggests that inclusive fitness benefits gained due to increased relatedness of nearest neighbors are not exceeded by increased kin-competition costs and female-biased dispersal, which makes it less likely that future offspring will compete locally with one another (Taylor 1992; West et al. 2002).

We do not have direct evidence that size is highly heritable in this species, but several lines of reasoning suggest that it is not. Our data show that high levels of relatedness do not correlate with similarity in male size, even though both are linked to lek size. Although traits associated with overall size have been shown to be partially heritable in other crickets (Simmons 1987), heritability estimates performed in controlled settings are often inflated (Simons and Roff 1994). Simmons (1987) showed that size is less linked to additive genetic variance for males than for females and thus more reliant on environmental effects, such as larval competition. It is possible that differences in soil moisture, botanical structure, and grazing/mowing practices may affect lek size and/or body size in the prairie mole cricket, but we have been unable to identify any patterns. Finally, it is likely that there is extensive gene flow between nearby leks due to a likely extensive flight range (Ulagaraj 1975). Both female mating flight behavior and the lack of relatedness-by-distance patterns for females suggest that populations of this species are not overly viscous (Figure 3).

It is unclear why the small leks in our study attracted a large number of females. Larger males tend to attract more females and have louder and lower frequency calls (Howard and Hill 2006). However, it is unlikely that females sample and move between more than 1 or 2 leks in a single evening, precluding much choice between leks. It is more likely that female dispersal patterns result from more passive effects, such as wind, or perhaps reduced acoustic interference on small leks enables the signal to travel further.

Although a higher attraction skew was seen on small leks, the actual mating skew for these leks is much lower, because males

would be unable to attract and mate with multiple females on the same evening. In large leks where females are a more limited resource, the effect of handling time is effectively 0 (very few males on large leks attracted multiple females in one night). Thus in a large lek, competition for mating opportunities with a nearby sibling is much more likely. On the other hand, due to the large number of females arriving in close synchrony on small leks, it is feasible that all males will mate on some nights, suggesting almost no competition for mates. We thus expect males on smaller leks to gain inclusive fitness benefits from displaying near relatives due to the likelihood that “spillover” females will mate with a related neighbor. It must be noted that the call characteristics potentially involved in female preference are still under investigation in this species. In any case, the benefit of remaining in kin groups must outweigh the potential costs. Indeed, the hotshot hypothesis in this system has found no support; previous findings show that male density is not correlated with attractiveness, and highly attractive males are located farther from the lek center than expected by chance (Howard et al. 2011). Male site selection is thus more likely a result of the lek botanical structure (such as grass height/biomass density, see Howard and Hill 2009).

Similarly, there would seem to be a clear benefit for males to disperse to smaller leks (more per-capita females, less competition). It is possible that males remain philopatric, because they are unable to assess their neighborhood due to sensory constraints (Howard et al. 2008; Pollack 1988), especially if they use substrate vibrations as a primary cue, which would place most neighbors out of sensory range (Hill and Shadley 1997, 2001). However, female field crickets clearly possess some mechanism to gauge density, as they have been shown to possess plasticity in response to the number of neighbors during both juvenile and adult life stages (Niemełä et al. 2012; Atwell and Wagner 2014). The fact that males on large, competitive leks do not disperse to more female-rich environments suggests either that they accrue benefits by remaining in kin groups or there are significant costs to dispersal.

An explanation for the clustering of kin groups that we have continued to explore is the possibility for cooperation (active or passive) among related neighbors. Spatial aggregation (Hill 1999) and male call adjustments in response to conspecific stimuli (Hill and Shadley 2001) provide compelling evidence that male neighbors do interact with one another. However, putative mechanisms for cooperation are presently unclear. It is possible that clustering of male relatives represents a passive response to patchy habitat, coupled with highly stratified female visitation patterns. If, as we expect, attractiveness is primarily based on the distance-dependent maximum call intensity, it might explain why males do not employ dispersal strategies to improve their mating success. Calling in a cluster of related males would increase the intensity of the collective sound produced and thus the probability a flying female could hear and locate the lek. While calling in a group of relatives, inclusive fitness benefits would be obtained even if an individual did not mate, but any spillover opportunities would increase the inclusive fitness of all those in the cluster. In each of these scenarios, clustering of male relatives at the closest nearest neighbor distances that we see in *G. major* (Hill 1999) is completely compatible with inclusive fitness theory.

Thus our data do not support the kin-selection hypothesis at the scale of the entire lek. The vastly divergent lek sizes and multiple scales of spatial aggregation often observed in the field for *G. major* suggest a complex system of female preference and male competition/cooperation, whether active or passive. Although females clearly do not prefer larger leks, the presence of male philopatry,

the likelihood of spillover matings, and increased male mass on small leks, where males are more highly related, suggest an alternative scenario based on inclusive fitness benefits between nearest neighbors and increased competition between kin clusters.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

This work was supported by Faculty Startup funds from the University of Tulsa (to WB) and the University of New Hampshire (to DRH), a Genomic Education Training Grant from LiCor BioSciences (to WB), the Nature Conservancy's JE Weaver Award (to KTK), and several Student Research Grants through the University of Tulsa's Office of Research and Sponsored Programs (to KTK).

We thank everyone who contributed to this project, especially those who helped in the field and in the lab. In particular, we are grateful to Elisabeth and Rachel Jorde for their assistance with fieldwork and data preparation. We also thank the Nature Conservancy and Robert Hamilton, Director of the Tallgrass Prairie Preserve, for encouraging research on preserve property and coordinating controlled burns and grazing to coincide with this project.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Keane et al. (2018).

Handling editor: Luke Holman

REFERENCES

- Atwell A, Wagner WE. 2014. Female mate choice plasticity is affected by the interaction between male density and female age in a field cricket. *Anim Behav*. 98:177–183.
- Bennet-Clark HC. 1987. The tuned singing burrow of mole crickets. *J Exp Biol*. 128:383–409.
- Bouzat JL, Johnson K. 2004. Genetic structure among closely spaced leks in a peripheral population of lesser prairie-chickens. *Mol Ecol*. 13:499–505.
- Concannon MR, Stein AC, Uy JAC. 2012. Kin selection may contribute to lek evolution and trait introgression across an avian hybrid zone. *Mol Ecol*. 21:1477–1486.
- Dunn OJ. 1964. Multiple comparisons using rank sums. *Technometrics*. 6:241–252.
- Figg D, Calvert P. 1987. Status, distribution and life history of the prairie mole cricket, *Gryllotalpa major* Saussure. Jefferson City (MO): Missouri Department of Conservation.
- Figg DE, Lister KH, Deitrich C. 1992. Population monitoring of the prairie mole cricket, *Gryllotalpa major* Saussure. Jefferson City (MO): Natural History Division, Missouri Department of Conservation.
- Freckleton RP. 2002. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *J Anim Ecol*. 71:542–545.
- García-Berthou E. 2001. On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. *J Anim Ecol*. 70:708–711.
- Gray DA. 1997. Female house crickets, *Acheta domesticus*, prefer the chirps of large males. *Anim Behav*. 54:1553–1562.
- Green AJ. 2001. Mass/length residuals: measures of body condition or generators of spurious results? *Ecology*. 82:1473–1483.
- Hahn DA. 2005. Larval nutrition affects lipid storage and growth, but not protein or carbohydrate storage in newly eclosed adults of the grasshopper *Schistocerca americana*. *J Insect Physiol*. 51:1210–1219.
- Harrison SJ, Raubenheimer D, Simpson SJ, Godin J-GJ, Bertram SM. 2014. Towards a synthesis of frameworks in nutritional ecology: interacting effects of protein, carbohydrate and phosphorus on field cricket fitness. *P Roy Soc Lond B Bio*. 281:20140539.
- Hayslip NC. 1943. Notes on biological studies of mole crickets at plant city, Florida. *Fla Entomol*. 26:33–46.
- Hill PSM. 1996. Reproductive ecology of *Gryllotalpa major* (Prairie Mole Cricket) [PhD Dissertation]. Norman (OK): University of Oklahoma. p. 92.
- Hill PSM. 1998. Environmental and social influences on calling effort in the prairie mole cricket (*Gryllotalpa major*). *Behav Ecol*. 9:101–108.
- Hill PSM. 1999. Lekking in *Gryllotalpa major*, the prairie mole cricket (Insecta: Gryllotalpidae). *Ethology*. 105:531–545.
- Hill PSM. 2000. Elements of the acoustic repertoire of the prairie mole cricket (Orthoptera: Gryllotalpidae: *Gryllotalpa major* Saussure). *J Kansas Entomol Soc*. 73:95–102.
- Hill PSM, Harrington W, Shadley JR. 2006. Singing from a constructed burrow: Why vary the shape of the burrow mouth? *J Orthoptera Res*. 15:23–29.
- Hill PSM, Shadley JR. 1997. Substrate vibration as a component of a calling song. *Naturwissenschaften*. 84:460–463.
- Hill PSM, Shadley JR. 2001. Talking back: sending soil vibration signals to lekking prairie mole cricket males. *Am Zool*. 41:1200–1214.
- Howard DR, Hill PSM. 2006. Morphology and calling song characteristics in *Gryllotalpa major* Saussure (Orthoptera: Gryllotalpidae). *J Orthoptera Res*. 15:53–57.
- Howard DR, Hill PSM. 2009. Grassland botanical structure influences lek spatial organization in *Gryllotalpa major* S. (Orthoptera: Gryllotalpidae). *Am Midl Nat*. 161:206–218.
- Howard DR, Mason AC, Hill PSM. 2008. Hearing and spatial behavior in *Gryllotalpa major* Saussure (Orthoptera: Gryllotalpidae). *J Exp Biol*. 211:3613–3618.
- Howard DR, Lee N, Hall CL, Mason AC. 2011. Are centrally displaying males always the centre of female attention? Acoustic display position and female choice in a lek mating subterranean insect. *Ethology*. 117:199–207.
- Hunt J, Brooks R, Jennions MD, Smith MJ, Bentsen CL, Bussiere LF. 2004. High-quality male field crickets invest heavily in sexual display but die young. *Nature*. 432:1024–1027.
- Isvaran K, Ponskhe A. 2013. How general is a female mating preference for clustered males in lekking species? A meta-analysis. *Anim Behav*. 86:417–425.
- Keane KT, Booth W, Howard DR, Golden TMJ, Hill PSM. 2018. Data from: competition decreases with relatedness and lek size in mole crickets: a role for kin selection? Dryad Digital Repository. <https://doi.org/10.5061/dryad.6q6r5>.
- Keane KT, Hill PSM, Booth W. 2016. The kin selection hypothesis in a lekking mole cricket: assessing nested patterns of relatedness. *Biol J Linn Soc*. 118:382–393.
- Kelly CD, Tawes BR. 2013. Sex-specific effect of juvenile diet on adult disease resistance in a field cricket. *PLoS One*. 8:e61301.
- Knapp M, Knappová J. 2013. Measurement of body condition in a common carabid beetle, *Poecilus cupreus*: a comparison of fresh weight, dry weight, and fat content. *J Insect Sci*. 13:6. Available from: <https://academic.oup.com/jinsectscience/article/13/1/6/1066000> (Accessed 24 May 2018).
- Kokko H, Klug H, Jennions MD. 2014. Mating systems. In: Shuker DM, Simmons LW, editors. *The evolution of insect mating systems*. Oxford: Oxford University Press. p. 42–58.
- Kokko H, Lindstrom J. 1996. Kin selection and the evolution of leks: whose success do young males maximize? *P Roy Soc Lond B Bio*. 263:919–923.
- Lebigre C, Alatalo RV, Soulsbury CD, Höglund J, Siitari H. 2014. Limited indirect fitness benefits of male group membership in a lekking species. *Mol Ecol*. 23:5356–5365.
- Loher W, Dambach M. 1989. Reproductive behavior. In: Huber F, Moore TE, Loher W, editors. *Cricket behavior and neurobiology*. Ithaca (NY): Cornell University Press. p. 43–82.
- Lydekker R. 1896. *The royal natural history*. London: Frederick Warne & Co.
- Marascuilo LA. 1966. Large-scale multiple comparisons. *Psychological Bulletin*. 69:280–290.
- McKight PE, Najab J. 2010. Kruskal-Wallis test. *Corsini Encyclopedia of Psychology*. Hoboken (NJ): John Wiley & Sons, Inc. p. 904.
- Newcombe RG. 1998. Two-sided confidence intervals for the single proportion: comparison of seven methods. *Stat Med*. 17:857–872.
- Niemelä PT, Vainikka A, Lahdenperä S, Kortet R. 2012. Nymphal density, behavioral development, and life history in a field cricket. *Behav Ecol Sociobiol*. 66:645–652.
- Nonacs P. 2000. Measuring and using skew in the study of social behavior and evolution. *Am Nat*. 156:577–589.
- Nonacs P. 2003a. Measuring the reliability of skew indices: is there one best index? *Anim Behav*. 65:615–627.
- Nonacs P. 2003b. Skew calculator 2003. Available from: <https://drive.google.com/drive/u/0/folders/0BzX3iYGMumwYbV9tdnJVaVMxYnc> (Accessed 24 May 2018).

- Pearson K. 1895. Note on regression and inheritance in the case of two parents. *P Roy Soc Lond.* 58:240–242.
- Petrie M, Krupa A, Burke T. 1999. Peacocks lek with relatives even in the absence of social and environmental cues. *Nature.* 401:155–157.
- Pollack GS. 1988. Selective attention in an insect auditory neuron. *J Neurosci.* 8:2635–2639.
- QGIS Development Team. 2012. QGIS Geographic Information System. Brighton: Open Source Geospatial Foundation Project. Version 2.6.1. Available from: <http://www.qgis.org/> (Accessed 24 May 2018).
- R Core Team. 2016. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: <https://www.R-project.org/> (Accessed 24 May 2018).
- Rantala M, Roff D. 2005. An analysis of trade-offs in immune function, body size and development time in the Mediterranean Field Cricket, *Gryllus bimaculatus*. *Funct Ecol.* 19:323–330.
- Raymond M, Rousset F. 1995. GENEPOP (web version): population genetics software for exact tests and ecumenicism. *J Hered.* 86:248–249.
- Regnaut S, Christe P, Chapuisat M, Fumagalli L. 2006. Genotyping faeces reveals facultative kin association on capercaillie's leks. *Conserv Genet.* 7:665–674.
- Ryder J, Siva-Jothy M. 2001. Quantitative genetics of immune function and body size in the house cricket, *Acheta domestica*. *J Evolution Biol.* 14:646–653.
- Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat Methods.* 9:671–675.
- Shorey L, Piertney S, Stone J, Höglund J. 2000. Fine-scale genetic structuring on *Manacus manacus* leks. *Nature.* 408:352–353.
- Simmons L. 1986. Female choice in the field cricket *Gryllus bimaculatus* (De Geer). *Anim Behav.* 34:1463–1470.
- Simmons LW. 1987. Heritability of a male character chosen by females of the field cricket, *Gryllus bimaculatus*. *Behav Ecol Sociobiol.* 21:129–133.
- Simmons LW. 1989. Kin recognition and its influence on mating preferences of the field cricket, *Gryllus bimaculatus* (de Geer). *Anim Behav.* 38:68–77.
- Simmons LW. 1990. Pheromonal cues for the recognition of kin by female field crickets, *Gryllus bimaculatus*. *Anim Behav.* 40:192–195.
- Simmons LW. 1991. Female choice and the relatedness of mates in the field cricket, *Gryllus bimaculatus*. *Anim Behav.* 41:493–501.
- Simons AM, Roff DA. 1994. The effect of environmental variability on the heritabilities of traits of a field cricket. *Evolution.* 48:1637–1649.
- Taylor PD. 1992. Inclusive fitness in a homogeneous environment. *P Roy Soc Lond B.* 249:299–302.
- Ulagaraj SM. 1975. Mole crickets: ecology, behavior, and dispersal flight (Orthoptera: Gryllotalpidae: Scapteriscus). *Environ Entomol.* 4:265–273.
- Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P. 2004. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Mol Ecol Notes.* 4:535–538.
- Walker TJ, Figg DE. 1990. Song and acoustic burrow of the prairie mole cricket, *Gryllotalpa major* (Orthoptera: Gryllidae). *J Kansas Entomol Soc.* 63:237–242.
- Wang J. 2007. Triadic IBD coefficients and applications to estimating pairwise relatedness. *Genet Res.* 89:135–153.
- Wang J. 2011. COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. *Mol Ecol Resour.* 11:141–145.
- West SA, Pen I, Griffin AS. 2002. Cooperation and competition between relatives. *Science.* 296:72–75.
- Wilk MB, Gnanadesikan R. 1968. Probability plotting methods for the analysis for the analysis of data. *Biometrika.* 55:1–17.
- Wilson DS, Pollock GB, Dugatkin LA. 1992. Can altruism evolve in purely viscous populations? *Evol Ecol.* 6:331–341.
- Zajitschek F, Hunt J, Jennions MD, Hall MD, Brooks RC. 2009. Effects of juvenile and adult diet on ageing and reproductive effort of male and female black field crickets, *Teleogryllus commodus*. *Funct Ecol.* 23:602–611.